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THE ORIGIN OF A SYMPATRIC SPECIES IN COLIAS THROUGH THE AID OF NATURAL HYBRIDIZATION

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I. INTRODUCTION

THE THEORETICAL SET UP for the origin of a new species in any biological group is the existence of two or more species in the same geographical area, which mix and reassort their combined gene combinations by the process of hybridization, F_1 intercrossing and backcrossing. There have been examples described in recent years in which crossing of this sort has served to blend together two existing species in a given area in such a way that both parental species cease existence as independent entities; this situation has been described generally as "subspecific intergradation" because of necessity the blending must be done on a geographical, or spatial, scale. Recent examples of this have been described by Sette (1962) involving the subspecies *macaria* and *laurina* of *Argynnis callippe,* and others by Hovanitz (1949).

In those cases in which natural hybridization of the two species has served only to permit gene (and character) interchange between the two original species, both of which maintain themselves as independent entities, but in which no new species is formed, the situation is described as one of introgressive hybridization. One of the most extensive cases of introgressive hybridization known is that existing between the species *Colias eurytheme* and *Colias philodice* (Hovanitz, 1943, 1944a, 1944b and 1948). Other cases which are less extensive are known in many other species of Colias.

Much more rare, possibly because the occurrence may be transient, is the situation in which two hybridizing species retain their separate existence, but out of the assorted gene pool arising by hybridization, there come a third species which maintains itself as a separate entity without the further necessity of hybridization. This is the situation to be analyzed in this paper.

It is almost axiomatic that *for closely related and interfertile species to exist in the same general area, and yet to maintain their separate identities, those two or more species must be separated in some way*

Fig. 1. North polar projection map showing the world distribution of *Colias hecla.*

by physiological or ecological isolation barriers for if this were not so, the genes of the two or more species would be blended together as in one gigantic melting pot. The isolation barriers for Colias appear to be such physiological and ecological ones rather than genetic ones since most species appear to be interfertile. Tied with these barriers is the selection for genes controlling adaptation for different habitats and different food plants of the larvae, which enable Colias to exist under a greater variety of conditions than would be possible were they all amalgamated into one species in a given geographical area.

Previous study has indicated that there is considerable natural hybridization in the genus Colias (Hovanitz, 1949, 1956). The species *Colias philodice* and *Colias eurytheme* have been shown to hybridize rather freely throughout all parts of their ranges where they are in

Fig. 2. North polar projection map showing the world distribution of *Colias nastes.*

contact, or where there is overlap of their habitats (Hovanitz, 1944a, 1944b). This is a classical example of *introgression, the reciprocal transfer of genes between two or more species in natural contact, but without the complete submergence of the identity of any.* Similar examples of natural hybridization have been described for the following species combinations of Colias:

Colias interior - C. christina
Colias hyale - C. erate - C. croceus
Colias christina - C. gigantea
Colias philodice - C. eurytheme
Colias hecla - C. nastes
Colias interior - C. philodice
Colias alexandra - C. philodice
Colias christina - C. philodice

Fig. 3. North polar projection map showing the world distribution of *Colias palaeno*.

Without doubt a great number of additional combinations will be found, wherever any two or more of the species of this genus occur together. Species hybridization in the laboratory, or in the field, leadnig only to F_1 generation individuals, with no history of fertile backcrossing or of fertile F_2 production, would have no effect on altering the composition of natural populations. Such crosses therefore are only indicative of physical ability to mate, of F_1 to survive (though not of F_1 fertility), and to indicate something of the nature of genetic dominance of the many characters involved in the cross; however, they give no information at all on the evolutionary relationships between the parental species. Further testing must be done for this purpose by carrying the crosses through to the F_2 generation and backcross generations, and by study of the genetics of the natural populations themselves.

Fig. 4. Distribution of *Colias hecla* in North America, together with that of *Colias meadi*. The ranges of these two species do not overlap but are separated at their closest point by an altitudinal difference of 4000 feet. *Colias hecla* is found in the mountains and plains of the north and *Colias meadi* only in the mountains of the south.

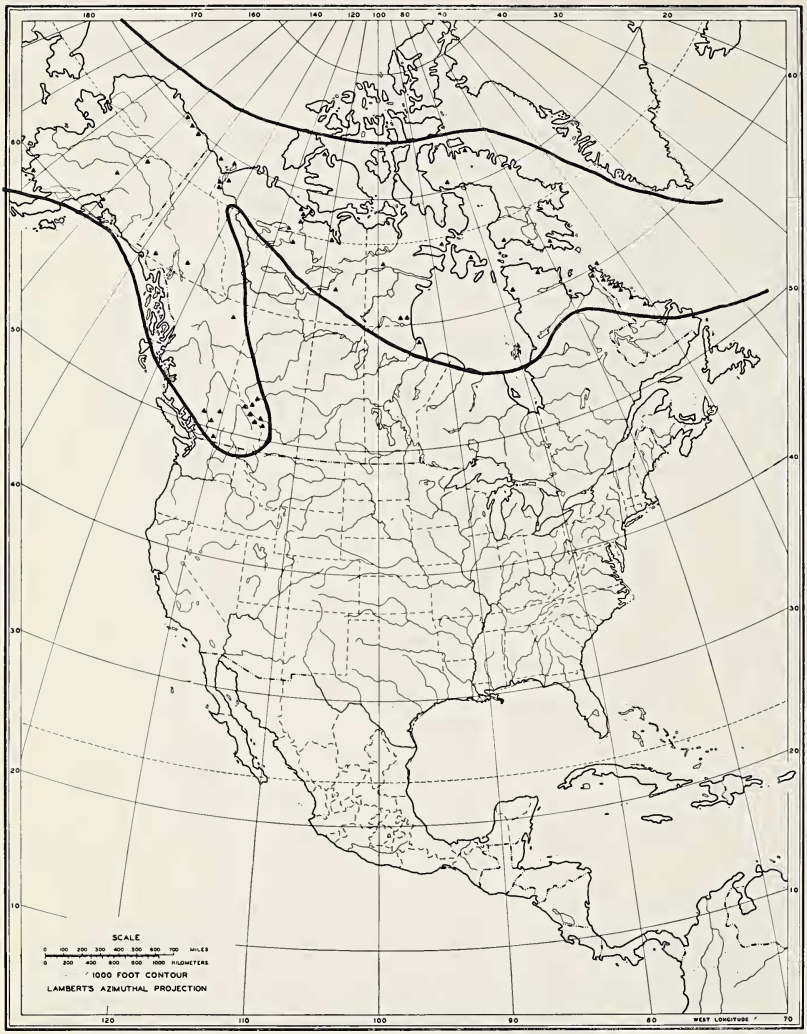


Fig. 5. Distribution of *Colias nastes* in North America. The species is found only in areas north of the tree line throughout the eastern and central parts of its range but occurs also far to the south in the western region of the Rocky Mountains in the alpine tundra.

It has been shown that *Colias hecla* and *Colias nastes* give all indications of hybridizing in the wild. These indications are as extensive as those which are known for *Colias eurytheme* and *Colias philodice* hybridizations, with the exception of a lack of the actual breeding experiments. In other words, the information is available by an analysis of wild populations, and character intergradation within the populations. It has been conjectured, in other publications, that these two species have hybridized in a certain area, namely the Canadian eastern arctic, in such a way and to such an extent, that a third species, *Colias boothi,* has originated as a result of such hybridization (Hovanitz, 1949). In the areas concerned, both parental species and the "intermediate" newly originated species all survive without the complete submergence of either parental species, or of the new species. The evidence indicates that on the fringes of the distributional area occupied by the "new species," intermediates are present in a way suggesting introgression only, rather than the independent existence of the new species. This "origin of a new species by hybridization" has been of theoretical significance in problems of evolution for many years; the present example is the first clear authenticated case of this type of origin which can be observed in action.

II. GEOGRAPHICAL RELATIONSHIPS BETWEEN *COLIAS HECLA, COLIAS NASTES* AND *COLIAS PALAENO*

The three most "northern" Colias in the world are *Colias hecla, Colias nastes* and *Colias palaeno,* the most northern of these three being first and *palaeno* being least northern. Although only the first two appear to be involved in the natural hybridization relationship, the third is considered here because of its frequent sympatric geographical distribution.

The world distributional ranges of these three species are shown in figures 1, 2, and 3. The North American ranges are shown in more detail in figures 4, 5 and 6. The latter three maps have been published previously (Hovanitz, 1951).

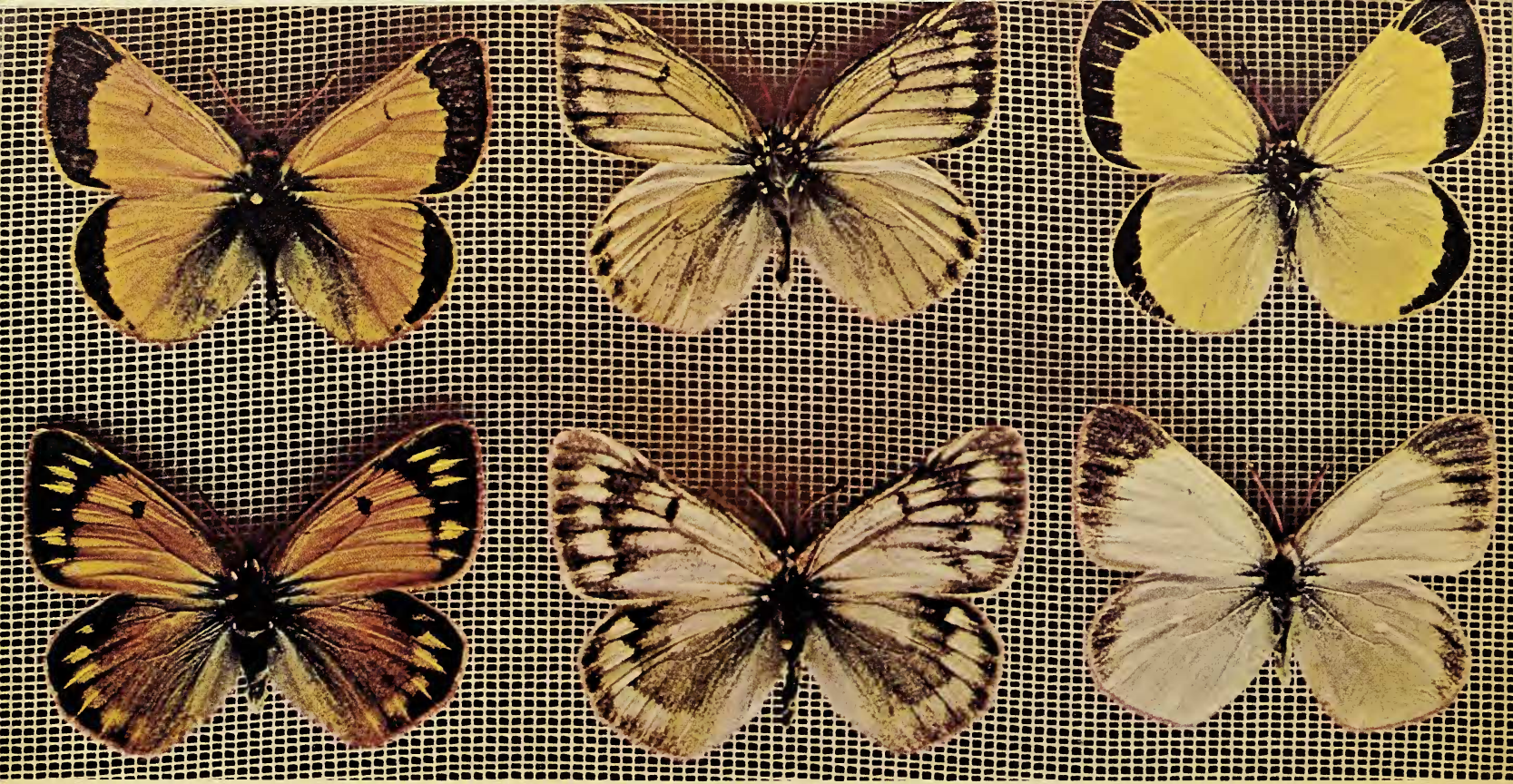
Colias hecla is distributed from northern Norway and Sweden across the arctic shores of Asia (fig. 1), across the Bering straits, across Alaska and northern Canada, throughout the Canadian arctic islands and around all coasts of Greenland. Southern extensions of range occur in several places around this circumpolar range. In Scandinavia, the species extends part way down the Sandinavian peninsula, but it does not appear in more southern European locations. In Asia, besides the coastal arctic locations, the species exists inland in the Verkhoyansk area and along the Lena river valley. Farther southwards, there is much material indicating the possibility of its existence in almost all ranges of central Asia including all the area from Hindukusch, Pamir and Karakorum across the Himalaya to Ladakh and mountains east and

north. The ranges extending north and eastward from the Pamir to the Baikal and Transbaikal completes a circle of mountains around the Gobi desert where some form of *Colias hecla* appears to live. Dots marking the exact locations for this area on the map were omitted because of the difficulty in every case to be certain of the identifications between the *hecla* group of forms and a group related to *Colias meadi* of the mountains of North America. Both of these groups appear to be in the same areas of central Asia, though they are separated in North America into contiguous regions.

In North America, *Colias hecla* is found in Alaska in all areas except the parts southern and coastal of the main southern mountain masses. This includes the mountains and valleys of the interior, and the western and northern coastal plains. In the Rocky Mountains, the species is found as far south as the present location of the Alaska highway from Whitehorse to Ft. Nelson but there are no locations known south of this point in the mountains area. The species then extends southwards on the Rocky mountain piedmont and the valley of the tributaries of the Mackenzie River as far south as Nordegg (just west and south of Edmonton, Alberta). The range skirts the prairie country of central Canada near Lake Athabaska, eastward to Fort Churchill on the Hudson Bay. The species is found on the most northern part of the Ungava peninsula and the upper tip of Labrador, but not along the Labrador coast. The map (fig. 4) in addition to showing the distributional range of *C. hecla* also shows the range of *C. meadi,* the relationship of which to *C. hecla* is uncertain despite its close phenotypic appearance.

Colias nastes has a distributional range only slightly more "southern" than that of *Colias hecla.* Actually, the ecological requirements of *C. nastes,* besides a temperature generally below 50°F., are somewhat different from that for *C hecla* as will be seen later. Unlike *C. hecla, Colias nastes* does not exist on any part of Greenland or the most northern of the Canadian arctic islands. Thus, on its circumpolar range, there is a break of great proportions across the Atlantic which does not appear on the map for *C. hecla. Colias nastes* is found in Scandinava in the same general locations as *Colias hecla,* extending part way down the mountain range. From there, it extends across the European and the Asiatic coastal sections (presumably) across the Bering straits to Alaska, along the north coast of Alaska and Canada to Victoria Island and Baffin Island but not to the islands to the north. In the islands north of Europe and Asia, *C, nastes* is known in Novaya Zemlya and has been listed as having been taken in Spitzbergen. Southwards, the species as such is not known in Europe, unless *Colias phicomone* of the Alps and the Pyrenees should be considered the same species. There seems little reason for not so considering it, in view of the fact that they are so similar in most respects. However, if they were connected in their distributional range at some earlier time, as

Fig. 6. Distribution of the *Vaccinium*-feeding *Colias* of North America. These include *Colias palaeno* of the mountains and plains of the northwest, *Colias interior* of the plains in the southern part of the range as well as the Cascade and Appalachian Mountains, *Colias pelidne* of the eastern arctic and the northern Rocky Mountains, and *Colias behri* of the alpine regions of the Sierra Nevada.



CENTER: *Colias nastes* ♂. same as above hecla only July 17, 1952. ♀. Karsavaggejakk creek, near Abisko, Sweden [Lapland], 900 m. elev. July 29, 1952. B. and W. Hovanitz.

Fig. 7. LEFT: *Colias hecla* ♂ and ♀. Jebrentjakko, near Abisko, Sweden [Lapland], elev. 7-900 m. July 25-26, 1952. B. and W. Hovanitz.

RIGHT: *Colias palaeno* ♂. Mile 691, Alaska Highway, near Rancheria, Yukon Territory. July 2, 1948. W. Hovanitz. *Colias palaeno* ♀. Alaska highway, 10 miles. South Burwash landing, Yukon Territory. July 1, 1948. W. Hovanitz.

Fig. 8. Series of Colias, mostly identifiable as *Colias boothi,* showing by means of a graded series, nine steps in the border pattern transformation from the male (or *hecla*) pattern at the top left to the female (or *nastes*) pattern at the second to the bottom right. Grades are designated as 8 through 4 on the left column and 3 through 0 on the right column. The specimen on the bottom right does not enter the series but is shown to illustrate a weak pattern development on a grade 0 male. All specimens shown are males and all are from Coppermine, Northwest Territories, Canada, July 12-19, 1947, W. Hovanitz coll. except: (1) 2rd from top on right column: Repulse Bay, Northwest Territories, Canada. July 21, 1950. P. F. Bruggemann. (2) 5th from top (last one) in right column, Repulse Bay, July 15, 1950. P. F. Bruggemann.

during the Pleistocene ice age, many thousands of years of isolation since that time has brought differences between them and earned a species distinction. Southward in central Asia in the ring of mountains surrounding the Gobi desert, including the Himalayas there is a string of races all of which appear to be specifically related to *C. nastes;* the main form here is known as *C. cocandica.* The map for *C. nastes* therefore has quite a similarity to the map of *C. hecla.* It can be seen however that in the area of Asia west of Sakhalien Island, *C. nastes* occurs considerably south of the area of *C. hecla.*

In North America, *Colias nastes* occurs also farther south than *C. hecla.* The species extends southwards in the Rocky mountains from the mountains of Alaska and the Yukon Territory to the borders of the United States in British Columbia and Alberta. In Alberta, *C. nastes* occurs at an elevation of 7500 feet and up while *C. hecla* is found at about 3-4000 feet in the piedmont. In these areas, *C. nastes* is flying in late July and August while *C. hecla* at the lower elevations is flying in May. *C. nastes* does not extend into the lowland valley areas of the Mackenzie tributaries as does *C. hecla* but instead is found only to the north of the tree line from the mouth of the Mackenzie to the area of Ft. Churchill on the Hudson Bay. It is found on the Belcher islands in Hudson Bay. It is found in the northern part of the Ungava Peninsula and then southeastwards along the Labrador coast half way down. The fost northerly known locality is on the northern coast of Baffin island. These locations may be observed in relation to one another on the map (fig. 5).

Though *Colias palaeno* is not involved in the specific study here being analyzed, it was thought that it might be so involved and therefore, its geographical distribution is here given together with the two preceding species. This species has a generally more southern distributional range than either *Colias hecla* or *Colias nastes* as can be seen by study of the world map (fig. 3). The species is found in the Alps of Europe, in a number of locations in the territory intervening between the Alps and the Scandinavian mountains, and northwards and eastwards. It does not exist far south of Lake Baikal in central Asia but does extend southwards into Northern Korea, on the island of Hondo in Japan, Sakhalien Island, and Kamtchatka Peninsula. The species is not known on the islands north of Europe and Asia. In North America, the species is known in Alaska south of the Brooks range and north of the main southern ranges which skirt the coast. It reaches the coast of Northern America only at the mouth of the Mackenzie river but extends southwards along the route of the Alaska highway to a point just north of Ft. St. John and thence eastwards to the Riding Mountains of Manitoba and northwards to the tip of the Ungava Peninsula. Its range is limited southwards and eastwards by contact with *Colias pelidne* (also called *interior*). For details on this contact zone, the map of North America is more precise (fig. 6).

III. CHARACTERISTIC DIFFERENCES BETWEEN *COLIAS HECLA, COLIAS NASTES* AND *COLIAS PALAENO*

Colias hecla may be distinguished readily from *Colias nastes* by the fact that it is always orange in wing color (fig. 7), while *Colias nastes* is pale yellow. *Colias palaeno* is more generally a brighter lemon yellow (fig. 7).

A second character that separates *hecla* from *nastes* but not from *palaeno* is a male-female dimorphism of the pattern. The male pattern is a single solid band of black on the outer edges of the fore and hind wings. This appears on the wings of the males of both *hecla* and *palaeno* (fig. 7). The female pattern on the other hand differes from this in a way that might be described as a series of dots in the border band, or in what might be the band when it is all present. This is typically shown for the females of *hecla* and *nastes* on figure 7. The band of the female of *Colias palaeno* is so reduced that the dots show only slightly in that species. The male of *Colias nastes* differs from any other North American species of Colias in that it also shows a series of dots in the border band, much like the female. In some cases, it is very difficult to distinguish the males from the females by general appearances.

Other differences in habit, larval food plant and ecological preferences will be discussed later in this series.

Intergradation between *Colias nastes* and *Colias hecla* as would be caused by hybridization, the crossing of F_1 to obtain the F_2 segregation and backcrossing should give a series of intermediate products with all intergradations from the one parental type to the other. In addition there should be produced, if the genetic segregation truly assorts itself with slight effects of genetic linkage, into truly divergent types such as a fully orange male with the female border band, a type found nowhere under natural conditions in the ordinary range of the species. Another type of extreme divergence which would be found only under such conditions of gene assortment would be a yellow form with the typically male border pattern. All these types have been found in areas of presumed hybridization of these two species, *Colias hecla* and *Colias nastes*. A series of variations ranging from the male border band to the female border band in a series of nine steps (grades) is shown in figure 8. A similar graded series of nine steps for the orange pigment on the upper side of the wings is shown in figure 9. These series are to be used to illustrate the analysis of various populations of Colias from diverse regions in the arctic.

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(to be continued)